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QUALITATIVE BEHAVIOR OF A PUPFISH (*CYPRINODON ATRORUS*) IN DIFFERING ENVIRONMENTS

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INTRODUCTION

Fishes have been used extensively by ethologists, and there are many papers that have contributed greatly to the understanding not only of fish behavior, but of general ethological theory as well (Aronson, 1949; Baerends and Baerends-Van Roon, 1950; Baerends, *et al.* 1955; Morris, 1958; Barlow, 1961a, *et seq.*; Nelson, 1964; Liley, 1966; Simpson, 1968; Miller and Hall, 1968; many others). However, since certain behaviors are modifiable (Hess, 1962; Marler and Hamilton, 1966), it is surprising that there are so few studies that compare a fish's behavior in differing environments. The present report describes qualitative differences in behaviors elicited by a pupfish, *Cyprinodon atrorus* Miller, in aquaria and in natural and semi-natural habitats.

MATERIALS AND METHODS

Cyprinodon atrorus inhabits saline marshes and lakes on the floor of the Cuatro Ciénegas basin, central Coahuila, northern México (Minckley and Itzkowitz, 1967; Miller, 1968; Minckley, 1969). Such habitats are severely variable, warming and cooling rapidly and subject to radical changes in salinities, dissolved oxygen, and so on (Minckley and Cole, 1968), and support only the most resistant biotic elements. *C. atrorus* is often the only fish species present at a locality, but another cyprinodontid, *Lucania interioris* Hubbs and Miller, and two poeciliids, *Gambusia longispinis* Minckley and *G. marshi* Minckley and Craddock, are sometimes abundant. Observations on the behavior of *C. atrorus* have been made at numerous places in nature, most intensively by Minckley and Elena T. Arnold in summer 1968. The activities observed were similar to those observed in a semi-natural pond (described below).

The pupfish used for study all originated from a stock caught in December 1963 from marshes associated with Laguna de San

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Pablo, 13 kilometers south-southeast of the village of Cuatro Ciénegas de Carranza, Coahuila, México. Seventeen individuals were placed in an artificial pool in March 1964, and by August a large, stabilized population had developed. It was studied intensively between 2 February and 30 April 1966. Breeding activities of this pupfish in nature begin in late January, intensify through early July, then decline to continue throughout the summer at a lower level. A second period of intense breeding activity often occurs in early autumn. The climate in Tempe, Arizona, is similar to that in the Cuatro Ciénegas area, and the fish also behave similarly. The semi-natural pond was isolated from disturbances in a large patio at Arizona State University. It was cement lined, but had a several-year accumulation of flocculent calcareous sediment. Considerable shade and organic input occurred from an overhanging mesquite (*Prosopis*), and city water continuously passed through the system. Maximum dimensions of the irregularly-shaped pool were 6 by 8 meters (m), and maximum depth was about 1.25 m (Fig. 1). Fishes were maintained without supplementary feeding. Observations were from a point about two meters above the water, by naked eye and through use of binoculars. Other vertebrates in the pond included poeciliid fishes, *Xiphophorus couchianus* (Girard) and *Flexipenis vittatus* (Hubbs), and a box turtle, *Terrapene coahuila* Schmidt and Owens. *Xiphophorus* were rare, *Flexipenis* built a large

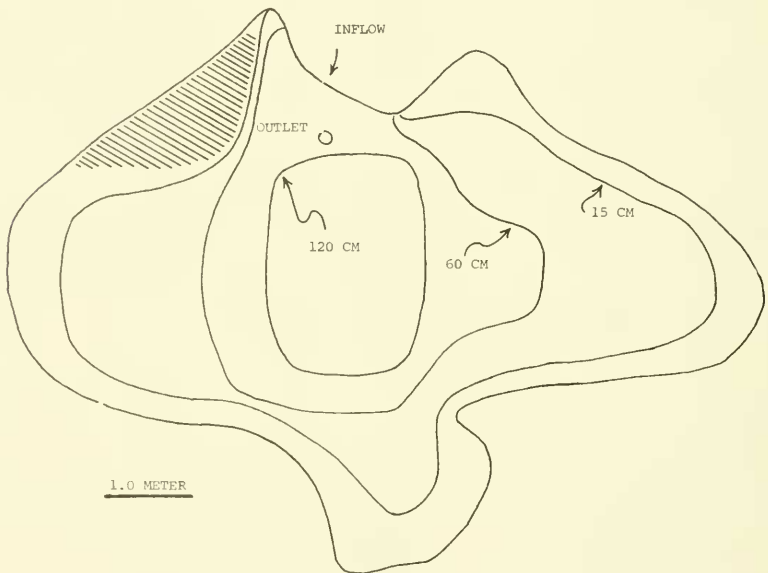


Fig. 1. Sketch map of the semi-natural pond at Tempe, Arizona, where *Cyprinodon atrorus* from the Cuatro Ciénegas basin, Coahuila, México, was studied. Contours are approximate, depths are in cm, and the hatched area is in the position of territories that were specifically observed.

population at the last of the study period, and the turtle was secretive during the day.

MOTOR PATTERNS

A behavioral sequence such as courtship consists of discrete motor elements (*e.g.*, muscle contractions) that occur with other such elements to produce synchronized patterns. Categorization is subjective since an observer must interpret the beginning and end of a given pattern, and evaluate variations. Major interpretive problems arise in description of numbers or intensities of components, or in the amount of time required for their completion. For present purposes, motor patterns making up broader behavioral sequences were weighted equally, and attempts were made to describe and evaluate variations. Where possible, names and definitions of patterns follow Barlow (1961a), as denoted by quotation marks.

Contacting.—"As the female moves slowly over the bottom the male stays beside her, and her head is usually just in front of his. Often they are actually touching."

Tilting.—"The female swims slowly within 0.5 centimeters (cm) of the bottom and tilts her body downward at an angle of 30° to 45° . All unpaired fins are spread. Barlow (1961a) considered this the beginning of nipping (see next), but in *C. a. torus* nipping may be omitted following a tilt.

Nipping.—"From the tilted position, the female opens her mouth, presses against the bottom, and normally takes up a mouthful of the substrate. . . . Then the body is dropped down against the bottom. When horizontal, the female either immediately spits out the substrate, or swims forward a short distance, stops, and then expels it." We include "halting" as described by Barlow (1961a) as a terminal component of a nip.

Sidling.—"The male swims forward and laterally against the female. The male's dorsal fin is folded or half open. The region supporting the anal fin of the male is thrust against the posterior line of the abdomen of the female. The body of the male is tipped out of the median plane only slightly, or not at all."

S-shaping.—"Seen from above, the body of the pupfish forms a gentle 'S' At this time the male and female normally lie side by side on the bottom in parallel S-shapes. The curvature is more pronounced in the male. The head and anal region of the male are directed toward the female, and the anal fin of the male is extended in her direction. The dorsal fin of the male is spread, and sometimes is bent slightly toward the female. In the female the dorsal fin is spread maximally. Moreover, her vent is pressed against the bottom and her caudal fin beats rapidly, but with a very small amplitude."

Wrapping.—"During S-shaping the male wraps his anal fin around the anal fin of the female."

Jerking.—"While still S-shaped the head is jerked toward the side opposite that to which it is already directed, thus initiating a wave of contraction which passes down the body reversing the direction of the S-shape. In the female one egg [or more] is extruded by this flexure, and the male presumably emits sperm at this moment."

Slow Rising.—"Both the male and female slowly rise from the substrate after a wrap. The female then moves away at high speed, and this is almost invariably the termination of spawning by the pair."

Patrolling.—"The male in his territory swims straight ahead in spurts of about 30 to 50 cm with the dorsal, anal, and pectoral fins folded back At the end of each spurt the male stops abruptly by throwing the colorful pectoral fins forward together in a quick movement that catches the eye. Then the male

stands momentarily with the median fins raised, and the pectoral fins beating alternately and rapidly. . . . Then he swims off again in a new direction. In this manner the male pupfish continually crisscrosses his territory."

Chasing.—An aggressive fish swims at high speed, often with its mouth open, toward a fleeing individual. If opportunity arises an aggressor will bite or butt a fleeing fish.

Lateral Display.—A fish spreads all its fins and presents its flank to another fish. The two fish often simultaneously present a lateral display in a parallel position, with bodies held head high and at an angle of 20° to 45° to the substrate.

Tailbeat.—Through use of the caudal fin a fish appears to push water against the side of another fish. Usually a lateral display is the beginning movement of a tailbeat; a more complete description was given by Barlow (1961a).

Following.—This pattern appears to have three basic variations that depend on the depth and speed of movement of a female and is subdivided for convenience as follows: 1) below—a female swims at slow to moderate speed with all fins extended, 10 cm or more above the substrate, and the male is either directly 2.5 to 3.0 cm below, or at a similar depth below, but behind, with his dorsal and anal fins half extended to completely depressed; 2) above—similar to "following below" except that the male is above a female, usually when the female is less than 10 cm above the substrate; and 3) in line—similar to "following above and below" except that the male is directly behind a female at any depth, and the female usually is swimming faster than when the other two patterns are utilized.

Looping.—There are five definable variations of looping. In all instances a male swims in a circle, semi-circle, or "figure-eight." 1) Below—a female in mid-water or near-surface, and stationary, often has a male directly below and swimming in a circle with all fins extended; 2) in front—a female may be at any depth, but usually at least 7.5 cm above the substrate with unpaired fins spread, and the male makes a circular loop or figure-eight directly in front or slightly in front and below; 3) to the side—similar to "looping in front" except that a male is to the side of the female; 4) sidle—a male assumes a sidle position (described above) then leaves a female to loop in front, then returns (most often on the other side) to continue a spawning sequence; and 5) zig-zag—a female stationary or moving slowly, with fins spread, is approached from a distance of 10 to 30 cm by a male performing continuous semi-circles (a male may also swim away making such movements, and in such instances the female may follow the male). The looping pattern, with many variations, also is used by territorial males in display against intruders.

Nuzzling.—This describes a motor pattern in which a male touches a stationary female with the anterior part of his body. 1) one—A male is below a stationary female and moves upward until the head and nape come into contact with, or slightly posterior to her branchiostegal region, then moves slowly back to the anal fin, around the side, and forward to a typical contact; 2) two—similar to "nuzzling one" except that a male moves directly to contact position without moving back to the anal fin; and 3) top—a male touches his lower head and breast to the dorsum of a female's head, then moves laterally and down to contact.

COURTSHIP AND SPAWNING IN THE ARTIFICIAL POND AND IN NATURE

The male of *Cyprinodon atropus* is a highly aggressive, vigorously territorial animal. The bright, iridescent blue body and contrasting yellow-orange fins, plus bold patrolling within a limited area, must make him conspicuous to other fish, and these features may also serve as a display to attract females that are willing to spawn. A female, when prepared to spawn, moves into a male's territory and nips the substrate. If the male is inattentive, the female may nip

several times, until the male approaches. Upon sighting a female, the motor patterns given above were scarcely evident in nature or in the semi-natural pond. The male swam directly toward the female at high speed, as if she were an intruder, or sometimes used a zig-zag loop in his approach. Moreover, most males immediately assumed a contact position, with no intermediary display. This was followed by a tilt and nip or a lunging nip by the female. The male sidled, both S-shaped, he wrapped, and both fish slowly rose. The female then swam from the territory at high speed, with the male following behind (a pursuit indistinguishable in such instances from a charge used when chasing an intruder). In totals of 116 observed spawns in the pond and 50 in nature that ended in a slow rise, this repertoire was invariable in sequence (Fig. 2).

One unusual series of observations were made of a pair "trapped" in a small area by surrounding clumps of filamentous algae. The male was exceedingly active, looping in front almost continuously then quickly contacting after the female nipped. The water was less than 1.5 cm deep, so a slow rise rarely followed a spawn. Both lay quietly for a second or so, then the female would dart forward with the male following in line. Algal mats blocked the female's rush, and she stopped after 3 to 5 cm. The male immediately began nuzzling and attempting to contact. This resulted in a nip and another spawn 12 of 33 times in a 31-minute period. The other times the female fled and dove into algae, followed by an active, looping search by the male. The female would re-appear, fanning her extended fins "nervously," and would nip or remain stationary. In the latter case she was immediately nuzzled and contacted, and nipped

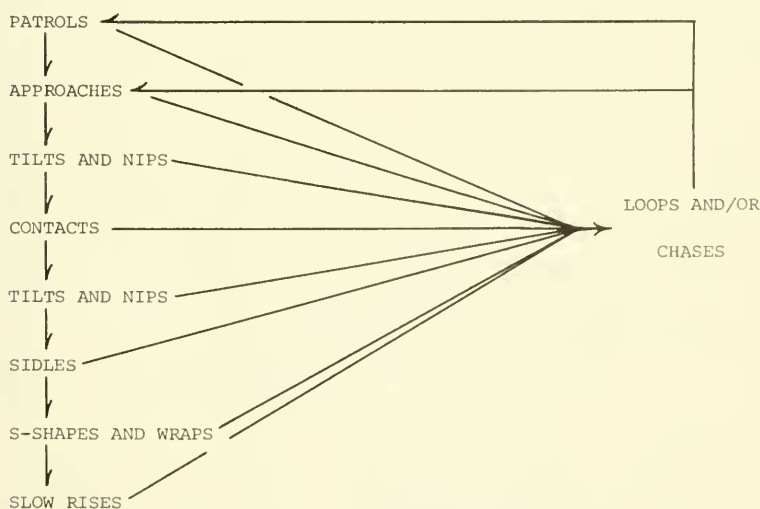


Fig. 2. Courtship and spawning sequences of *Cyprinodon atrorus* in natural and semi-natural habitats.

and spawned or again fled to hide. No other observations of nuzzling have been made under field conditions, and no such hyperactivity has otherwise been noted in *C. atrorus* under natural or semi-natural conditions.

In any stage of a reproductive sequence a male would leave a female to challenge an intruder. In the pond between February and late April about 50 percent of the females that nipped the substrate in a male's territory failed to spawn, and most times this resulted from interruption by other fishes. No quantitative data are available from observations in nature, but disturbances of a similar nature were often seen. While some discrimination by a non-spawning male between homo- and heterospecific interlopers was evident, no such recognition was obvious when a male was interrupted during a spawning sequence. Even intruding poeciliids were aggressively driven from the area when a defender was spawning, as were young *C. atrorus* that are oftentimes ignored by defending males. Since looping also occurred when no interlopers were present, or when a male was returning to a female after chasing, it may also serve to pacify a "nervous" female or to block her retreat from the spawning area.

The motor patterns of tilting, jerking, following above, and following below were not observed in the pond or in nature.

COURTSHIP AND SPAWNING IN AQUARIA

Male and female *Cyprinodon atrorus* were first kept isolated for a number of days in separate, 28-liter tanks (35 by 26 by 22 cm), then a male was introduced into a female's tank. Upon introduction, a male always initially sank to the bottom, or moved into a position along a wall. The female also would sink to the substrate, with all fins extended. The female initiated activity, swimming to the male and tilting and/or nipping the substrate nearby. If a male was inattentive a female would "mildly" butt or bite at his body. Males sometimes responded to such aggression with tailbeat, and if this occurred the female always retreated. When a nip occurred the male usually swam directly to a contact position. Typical behavior consisted of a variable period of contact, followed by a sequentially-inconsistent assemblage of motor patterns on the part of the male that eventually terminated in a spawn (Fig. 3). On the average, in 668 observed spawns, a sequence of contact → tilt and/or nip → S-shape → wrap → jerk or slow rise predominated (Fig. 4).

Females under conditions of aquarium isolation often remained receptive to a male after the initial spawn. Females with high sexual tendencies spawned immediately after the pair was placed together, then began swimming slowly through the tank, conveniently accessible to the male. This is not the case in nature since a female immediately leaves the male's territory after the spawn is consummated. The presence and "receptivity" of a female stimulated hyperactive sexual behavior on the part of a male, such as nuzzling, looping, and following. These displays had little if any sequential cor-

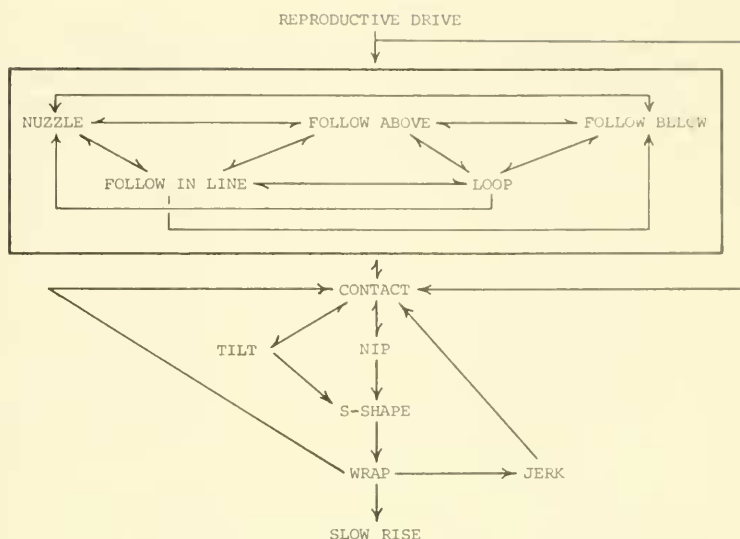


Fig. 3. Relationships of courtship and spawning motor patterns of *Cyprinodon atrorus* in laboratory aquaria.

relation to one another or to other patterns (contacting, nipping, etc.) of a more terminal spawning sequence. However, 41 percent of the courtship patterns (whatever they were) led directly to a second spawn. The behavior, notwithstanding its variations, must therefore have succeeded in stimulating the female to continue reproductive activities. When a female was not initially prepared to spawn, a similar series of random patterns was produced by a male. However, it was rare for a male to induce an initially unresponsive female to spawn.

The male *C. atrorus*, when territorial, is always receptive to a female, and the female controls spawning by presenting herself within a territory and performing the nipping pattern. The female apparently requires little stimulation by a male (excepting, perhaps, a short period of contacting, or some visual stimulation from male defensive activities) when she is prepared to spawn. Random use of courtship motor patterns appears to function in stimulation of a female to continue the spawning activities, rather than as an initiator. Rigid courtship sequences require reciprocal stimulation, and randomness of behavior of male *C. atrorus* may result from a lack of cues from the female.

TERRITORIALITY IN THE SEMI-NATURAL POND AND IN NATURE

Males of *Cyprinodon atrorus* begin to establish territories in late January, and remain aggressive throughout the breeding season with the intensity of behavior varying with intensities of reproductive activities in the given habitat. Males began sporadic aggressive ac-

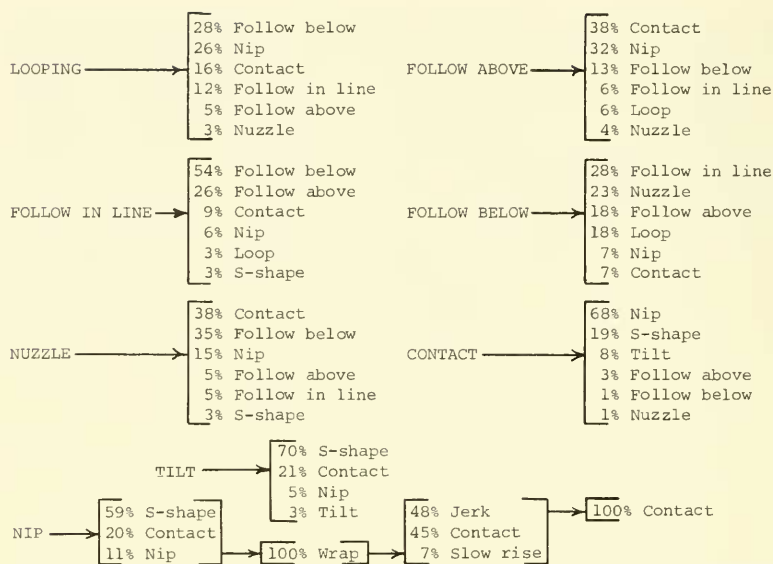


Fig. 4. Quantitative relations among a motor pattern and those patterns observed to follow it in *Cyprinodon atrorus* under laboratory aquarium conditions, based on 668 observed spawnings.

tions in February in the artificial pond. Fights were not confined to a particular area, and usually consisted of short charges with little or no contacting. Some fighting was associated with feeding pits during this period, an activity continued almost throughout the year by non-reproductive males, females, and juveniles (Minckley and Arnold, 1969). Pit-building and defense is unrelated to reproductive activities in *C. atrorus*, although it may have significance in the sexual behaviors of some other pupfish species (E. T. Arnold, pers. comm.).

In mid-February, several males established temporary areas in shallows of the semi-natural pond, but these were not defended for more than a few hours. They were 15 to 25 cm in diameter in water not more than 5 cm deep. Boundaries were ill-defined and frequently changed more than five cm in a few minutes. Border fights between neighboring fish rarely occurred since territories were widely dispersed and usually isolated. Permanent territories were formed by late mid-February, and three, well-defined, adjacent ones were selected for intensive observations. These were situated in a cove that sloped gently to a maximum depth of eight cm. On the pondward side was an abrupt slope leading to water more than 30 cm deep. The territories were at depths between 2 and 8 cm (Fig. 1), and occupied all available shallow water. The largest included about 2,100 square centimeters (cm^2) and the smallest was 1,050 cm^2 in size. The range in estimated sizes for territories in nature is 3,200 to 875 cm^2 (23 estimates), with a mean of about 1,950 cm^2 . Shapes of

territories ranged from round in open, sparsely populated areas, to elongate and highly variable where heterogeneity of habitat, or the presence of other males, influenced the boundaries. The three males in the pond vigorously defended their respective areas until mid-March. Others then began to form peripheral territories, and wedges defended by new males were progressively forced into and between the three original ones. The three defended areas were markedly compressed to about half their original sizes, and within a week the fish had been displaced and disappeared.

Territorial defense by *C. atrorus* consists of numerous lateral displays, infrequent tailbeats against peripheral males, and charges against non-territorial males and sometimes females and juveniles. Actual contacts and severe fighting occur when territorial boundaries of "matched" males (in size and coloration) are closely appressed, especially when the border meets in relatively deep water (>5 cm). Under such conditions the males present sustained lateral display, tailbeat, and biting, the last generally in the vicinity of the anal fin and flanks. Contact fighting, although rare, usually begins near the surface, and the two males spin about each other as they gradually move toward the bottom. Fights are sustained for as long as 30 seconds, and a small cloud of sediment often obscures the terminal phases of such conflict. Tinbergen (1953), Carranza and Winn (1954), and Miller (1964) have noted that the ferocity of attack by a defending male of fishes they studied (*Gasterosteus aculeatus* Linnaeus, *Fundulus notatus* [Rafinesque], and *Trichogaster trichopterus* [Pallas], respectively) increased as the interloper more closely approached the territorial mid-point. However, this type of differential aggression did not obviously occur in *C. atrorus*. The defending male appeared to attack all intruders (excepting young and reproductively-oriented females) with equal aggressiveness, regardless of their distance from the center of this area.

TERRITORIALITY IN AQUARIA

Results from a number of experiments with *Cyprinodon atrorus* in aquaria are similar, and only one is described here. A bare, sand-bottomed, 160-liter tank was used to attempt to duplicate the territorial sequences observed under field conditions. Seven adults of generally equal size, 3 males and 4 females, were placed in the tank, and they immediately formed a tightly-knit, stationary cluster (a "pyramid") near the substrate. They remained in that position for several minutes, then began exploratory swimming. When disturbed they immediately returned to a pyramid cluster. By the second day the fish began to seek individual refuge when disturbed. There was sporadic aggression, not limited to any particular area. On the third day one male defended a small area near the substrate for a short time. At the end of the first week, one male rigorously defended the entire bottom of the tank, from the substrate to about eight cm above, making frequent forays against fish positioned at higher levels. When attacked, other fish fled without defensive display. At

the end of the second week another male began to defend a 10- by 38-cm area at one end of the tank, positioned about 8 cm above the bottom and extending to the surface. This was defended against all but the male who continued to patrol the substrate. The third male did not establish an area, and was intimidated by both other males. There was continual, mild, aggressive activity among the females, and they often attacked the subservient male. None of the female attacks was prolonged, but consisted merely of a short charge terminating in a butt or bite. The hierarchy in males was maintained for a month, when the experiment was terminated. These results are similar to those obtained by Barlow (1961a) for *Cyprinodon macularius* Baird and Girard, and have been duplicated in our laboratory using a number of other pupfishes.

DISCUSSION AND CONCLUSIONS

The study of behavior of fishes in the wild is exceedingly difficult, and the abundance of variables existing under field conditions makes it simple to overlook significant factors and to arrive at spurious conclusions. In the laboratory, new factors are introduced by creation of "standard conditions," and data acquired from fish in aquaria may be equally misleading.

Behavior of *Cyprinodon atrorus* in natural and semi-natural habitats lacked many components that were commonly present under aquarium conditions. Nuzzling, for example, generally occurred only when a stationary female was 10 or more cm above the substrate, and when she remained for some period of time in a male's territory. Since all territories in nature or in the pond were in water shallower than eight cm (and usually less than five cm), physical limitations precluded performance of the pattern. The absence of following (especially above and below) under field conditions may also be attributable to insufficient depths. In addition, females in the pond did not remain in the territory after a spawn, but moved away at high speed so that little time was allowed for the male to perform complex display patterns (with the notable exception discussed on page 00).

The lack of records of the jerk motor pattern in nature and in the pond is confusing. Barlow (1961a) implied that this was correlated with passage of gametes; since young were abundantly produced in the semi-natural pond, a jerk is obviously not essential for successful reproduction. The jerk motor pattern in aquaria always led to a continuance of spawning (Fig. 3), and only a slow rise resulted in its termination. However, on the one occasion when repeated spawning by a pair of fish was observed under field conditions (p. 00), the female did not jerk, and repeatedly utilized a slow rise (or a period of quiescence in shallow water) after spawning.

Tilting is difficult to observe from above, and may be physically impossible for a female in shallow water, and these factors may explain its almost-complete absence from the behavioral repertoire

in the pond. Highly motivated females in aquaria always tilted, but often omitted a nip in their pre-spawning movements.

The abbreviated, "to-the-point" spawning sequence under natural conditions, highly stereotyped and almost invariable, may be a result of the over-riding territorially of the male *C. atrorus*. A male will curtail spawning at any point to chase an intruder in his territory. When a pair is placed in a habitat devoid of other fishes the barraging effect of stimuli from interlopers is removed and the pair may receive and react to other facets of their immediate surroundings. Sexuality becomes the only broad stimulus, and subtleties of activities on the part of each fish create a diversity of reactions in each. Variability in their behavioral repertoires, such as occurs in aquaria with the appearance of several courtship patterns, may then ensue. This is supported somewhat by the diverse behavior exhibited by the pair of fish isolated under semi-natural conditions by algal mats (p. 00).

Development of territorial behavior in the laboratory is very similar to that occurring under field conditions. Sporadic fighting precedes acquisition of temporary territories, and fixed territories remain relatively permanent. The artificial confinement in a tank allows (or forces) development of a hierarchy. If these occur in nature they are highly complex and localized. Males unable to hold or establish territories in nature remain in deep water and avoid contact with aggressive individuals, and smaller males sometimes defend stones or vertical banks in peripheral areas. These kinds of behavior correspond generally to the activities of the non-dominant males in aquarium situations.

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